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THE EARLY DEVELOPMENT OF DESMOGNATHUS FUSCA.¹

HARRIS HAWTHORNE WILDER.

IN a former number of the *American Naturalist* (March, 1899) I presented what seem to have been the only published observations on the development of one of our commonest and most generally distributed salamanders, *Desmognathus fusca*, but as I was then unable to describe the early stages, a most essential gap in this history remained unfilled.

The eggs which furnished the object of my former sketch were laid in the laboratory terrarium on or about June 1, 1898, but as the first observations were made on them June 11, at which time they were in the form of well-formed embryos coiled about enormous yolk-masses, the first eleven days of the development remained unknown, a period which includes the extremely important cleavage stages, the formation of the blastopore and the beginning of the head and tail folds.

Since that time a number of specimens of *Desmognathus* have been kept in our terrarium each spring, and the favorite hiding-places investigated daily during the egg-laying season, but with no success until the present year (1903) when on June 22 at 1.00 P. M., there was found a batch of twenty freshly laid eggs associated with a small but evidently mature female. At this time the eggs were in the early cleavage stages, and varied from the two-celled stage with the second cleavage forming to that of 16 cells, as represented by the first five rows of Fig. 1. Nine of these were preserved at once in 5% formaline, and the remainder were killed, one or two at a time at intervals representing the most important stages. The eggs were, however, rather few in number, and in spite of considerable conservatism in the daily sacrifice, there were but two left when cleavage was com-

¹ From the Zoological Laboratory of Smith College.

pleted and the blastopore was about to be formed. These two, compelled on June 27 to make a journey with me to Maine, in spite of the utmost care, did not survive the hardships of travel and the experiment came to an end. I am thus able to record the development only during the first three days of existence, leaving the period from the fourth to the eleventh still unknown save through analogy with allied forms, and waiting to be written when occasion may offer.

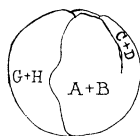
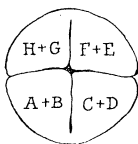
This early history includes only surface study, mainly of preserved material, but seems to be of especial importance as showing a genuine holoblastic type of cleavage when from the later form of the embryo a meroblastic form was to have been expected.

The various cleavage stages are represented in Fig. 1, in which the first perpendicular column represents them as seen from the upper pole, the second from the side, and the third from below; the figures in each horizontal row representing several views of the same egg. Of these stages the first five occurred simultaneously at the time the eggs were found, 1.00 P. M. June 22, and as no eggs were found the day before, they probably represent stages of 6-15 hours, resulting from eggs laid at intervals during the preceding night.

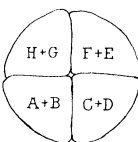
The successive changes and the descent of the various cells seem evident, and may be traced with an approximate certainty as far as the 23-cell stage, as indicated by the lettering. In the first stage shown, the first cleavage is complete, separating the egg into its two halves, A + B + C + D and E + F + G + H, while the second cleavage, beginning at the upper pole, has proceeded nearly to the equator and is separating the halves into the components A + B, C + D, E + F and G + H, a stage which is seen completed in the second row.

The third cleavage, at least in the eggs examined, is not the typical horizontal one which might be expected, but consists of a set of four meridional ones, which start near the upper pole as so many separate fissures from one of the two former cleavage planes, probably the first. Similar fissures were observed in one instance near the lower pole and it is evident that those from above and those from below meet one another, and result

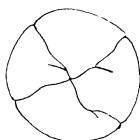
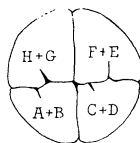
1st cleavage completed,
2nd cleavage begun,
June 22, 1.00 P. M.
[The eggs were found
at this date, and then
presented various
stages, from this to
that of 16 cells.]



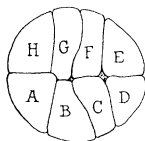
2nd cleavage com-
pleted, 4-celled stage.
June 22, 1.00 P. M.



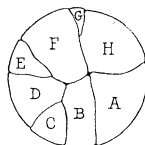
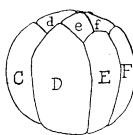
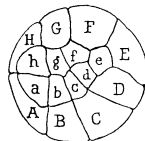
Beginning of 3rd cleav-
age. June 22, 1.00
P. M.



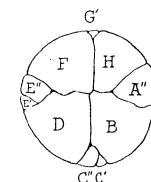
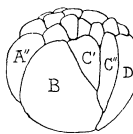
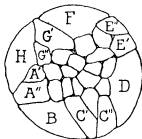
3rd cleavage completed,
8-celled stage. June
22, 1.00 P. M.



4th cleavage completed
16-celled stage. June
22, 1.00 P. M.



28-celled stage, with 16
micromeres, 12 mac-
romeres. June 22,
4.30 P. M.



42-celled stage, with 26
micromeres, 16 mac-
romeres. June 22,
11.00 P. M.

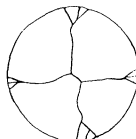
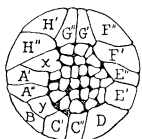


FIG. 1.—Eggs of *Desmognathus fusca* [1903 material]. Segmentation stages, observed June 22, between 1.00 and 11.00 P. M. The left-hand column shows upper poles; the next side views; and the right-hand one, lower poles. $\times 6$.

in the formation of an eight-cell stage, which is bilateral along the plane of the first cleavage, and consists of the four cells A. B. C. and D. upon one side, and of E. F. G. and H. on the other (fourth row of Fig. 1). These eight meridionally arranged blastomeres do not seem to have equal value in respect to size, for through a slight obliquity in these four new lines of cleavage there result four smaller blastomeres which alternate with four larger ones, and of these the latter alone usually attain the lower pole while the former ones do not reach it. This is seen by a study of the lower pole views in the fifth and sixth rows of Fig. 1, where the smaller blastomeres A. C. E. and G. intrude like wedges along the lines of the first two cleavages, but do not reach the pole save in the single instance of A. in the fifth row, an unusual condition.

The next cleavage is an horizontal one, forming an approximate circle about the upper pole, and cutting off small segments from each of the eight blastomeres of the preceding stage (fifth row). This results in a 16-cell stage, consisting of eight micromeres, a, b, c, etc., clustered about the upper pole, and eight macromeres, the remaining parts of the original cells. This last cleavage takes place so far above the equator of the egg that it does not change the aspect of the lower half, and thus the drawing of this egg (the third of the fifth row) would answer equally well for the preceding one.

By a comparison with Eycleshymer's studies of *Amblystoma*, (*Journal of Morphology*, Vol. X, 1895) it becomes evident that this latter cleavage is the one which is described as typically the third in Amphibian eggs, and that the four meridional cleavage lines which result in the formation of the 8-cell stage, together form the usual fourth. Indeed, this transposition of the two cleavages occasionally occurs in *Amblystoma*, and as my observation rests upon the study of but two eggs, it cannot be asserted that the order described is the typical one in *Desmognathus*. It is, however, identical with the method shown and figured by Kerr in *Lepidosiren*, and his figures of the third cleavage (by means of the four short lines) as copied by Ziegler (Figs. 213-314 of his *Entwicklungsges. der niederen Tiere*. 1902) would serve in every respect as better pictures of *Des-*

mognathus eggs in the corresponding stages than I have been able to draw. The occurrence of the third meridional before the horizontal cleavage seems also to be the rule in *Acipenser* and in *Amia*.

The next stage, that of 28 cells, is shown in the sixth row, and appears to consist, first, of a division of each micromere, increasing their number to 16, and, secondly, of a longitudinal division of the smaller macromeres A, C, E, and G, into A'. A'' C'. C'' etc., while the other four B. D. F. and H. remain undivided. The subdivisions of the smaller macromeres may or may not be visible from the lower pole, as is seen in the third figure of the row.

Beyond this the subdivisions cannot be followed with certainty, but the last figure shown (seventh row of Fig. 1) which consists of 26 micromeres and 16 macromeres, 42 in all, appears in some

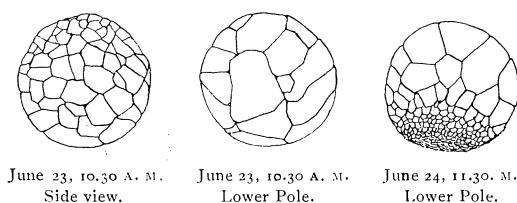


FIG. 2.—Eggs of *Desmognathus fusca* [1903 material]. Later segmentation stages, representing a direct continuation of the series shown in Fig. 1. $\times 6$.

respects to show some regularity, although in others it is disappointing. We would expect, indeed, to account for the increase from 12 to 16 macromeres by a subdivision of each of the remaining ones, B. D. F. and H, but while this can be seen to be the fact in the case of F and H, the two other new macromeres cannot well be explained by a subdivision of B and D. Instead of this, they appear as those marked x and y, and the relation of those and of B and D to the smaller intruded macromeres is such as not to allow the desired interpretation. Less difficulty appears in the interpretation of the 26 micromeres, for while we would naturally expect a doubling of each of the 16 of the former stage, and a consequent 32 in this, its smaller number may well be accounted for by the supposition that some of the original 16 have not yet divided. No definite interpretation

can be made, however, for this 42-cell stage, since but a single specimen was available for study, but it may be seen from the above sketch of this and the preceding stages that the eggs of *Desmognathus* will furnish a very interesting and convenient object for the study of cleavage problems in Amphibia.

Sketches of two later cleavage stages are given in Fig. 2 and may be seen to consist of a greater and greater subdivision of both micro- and macromeres, apparently without special regularity. The last figure (June 24) represents the lower pole of the oldest stage I succeeded in obtaining.

The above observations, which establish the fact that the

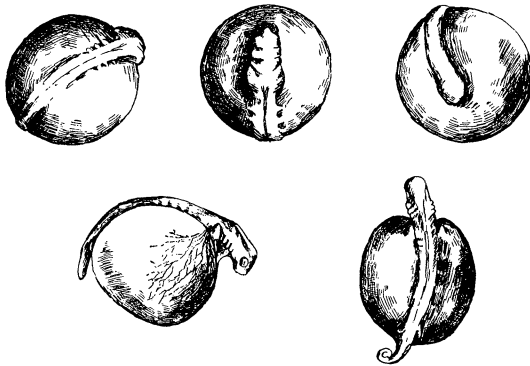


FIG. 3.—Early embryos of *Desmognathus fusca* [1898 material]. The figures in the upper row represent different aspects of a single egg of the stage described in the previous paper as "A." Similarly, the two figures of the lower row represent different aspects of the stage described primarily as "B." $\times 6$.

eggs of *Desmognathus* are holoblastic, will serve to correct the statement to the opposite effect given in my previous article on the subject, and while it is always unpleasant to be proven in a mis-statement, it is more satisfactory to the investigator to be able to furnish his own proof than to leave it to others. At the time of writing my previous article, I possessed no embryos younger than those represented in the upper row of Fig. 3, and it then appeared to me impossible that such a relation between embryo and yolk as the one shown here could result from an egg of the holoblastic type. A slightly older stage, that represented in the second row of Fig. 3, seemed still more convincing in this respect, since by this time a set of branching blood vessels

had made their appearance on the surface of the yolk, reminding one forcibly of similar embryos *e. g.*, those of certain Teleosts, that result from meroblastic eggs. Too sharp a distinction between the holoblastic and meroblastic type cannot, however, be drawn, since there are numerous transition forms, as that of *Salamandra maculosa*, in which the egg is 4–5 mm. in diameter, and the first two cleavage planes, although they slowly cut their way around the egg on the outside, often fail to divide the yolk internally, “so dass die Furchung in den ersten Stadien partiell ist” (Ziegler *loc. cit.*, p. 249, on the authority of Grönroos, 1903). A similar condition has been produced experimentally in the frog’s egg by O. Hertwig (1897). The eggs of the Gymnophiona, which are the largest of all Amphibian eggs, (7–8 mm. in *Hypogeophis rostratus*) are at first typically meroblastic, with a germinal disk that spreads gradually over the yolk; but during and after gastrulation the yolk becomes divided up into large cells, so that the eggs are ultimately holoblastic.

In these latter, also, as well as in the eggs of *Salamandra* and *Desmognathus*, there is a noticeable array of blood vessels upon the yolk, which at first sight closely resembles a true yolk circulation, but which in reality consists of the vessels which normally appear superficially in the region distended by the yolk mass, and thus, although they may receive nutriment from the yolk, they are in no sense true vitelline vessels. The veins of this region, though not the arteries, could be closely followed in the two series from which Figs. 4 and 5 were taken, and are shown to be three in number, one median and two lateral. The median vein lies along the mid-ventral line of the swollen abdomen, scarcely noticeable posteriorly, but increasing anteriorly as it picks up several lateral branches. It passes along the dorsal (concave) aspect of the liver and enters the sinus venosus in company with the hepatic vein. By its position and course it undoubtedly corresponds to the abdominal vein of the adult, and thus, although it may be also a potential portal, it cannot be very definitely related to the true vitelline veins of meroblastic embryos. In the same way the two lateral veins are seen to be identical with the large cutaneous veins which lie along the sides

of the trunk. They empty into the *Ductus cuvieri* near the entrance of the subclavian.

Thus, although it is seen that many Amphibian eggs are on the border between the holoblastic and meroblastic types, and although they form interesting transitions between the two, especially useful in breaking down artificial distinctions, yet it must be confessed that through the observations here recorded the eggs of *Desmognathus* are at first almost typically holoblastic, although in the later relation of embryo to yolk they greatly resemble meroblastic embryos. (cf. Fig. 3 of this paper with the following in Ziegler's text-book, 1902, Fig. 304.) *Hypogeophis* (Brauer); Fig. 188 herring (Kupffer).

In concluding this paper I wish to present a few sections

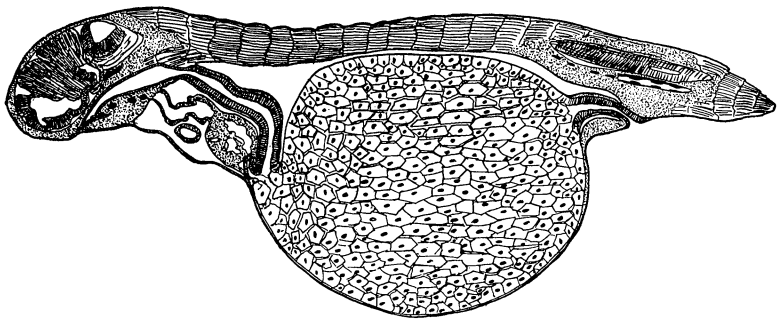


FIG. 4.—Sagittal section, a little to one side of the median line, of an advanced embryo of *Desmognathus fusca* [1898 material] a little older than "Stage D" of the previous paper.
X 15.

taken through advanced embryos of *Desmognathus* (the 1898 material) which will show the actual relation of the embryo to the large yolk mass and will demonstrate its cellular character in the later stages.

Fig. 4 is a sagittal section of an advanced embryo, and shows the median relationships in the ventral half, but strikes the brain and the dorsal portion somewhat laterally. By combining several adjacent sections, the pharynx, œsophagus and anus were completed. In this the peritoneum may be followed dorsally as a continuous line investing the rectum, the yolk mass and the œsophagus, and enclosing a portion of the cœlom; and ventrally around the yolk mass enclosing a large cœlomic space

ventral to heart and liver and a smaller one ventral to the anus. The entire yolk mass, which is wholly cellular, is enclosed within the peritoneum and is morphologically the equivalent of the middle portion of the intestinal tract in which a lumen has not as yet appeared. Fig. 5 shows four cross-sections of an embryo a little older than that of Fig. 4 and taken from a single series, the first through the liver, the second through the yolk at its greatest circumference, the third through the hip-girdle and rectum and the fourth through the cloaca, with the hind-limbs at the side. The numbers attached to each are those of the sections as numbered in the series. These show the same relationships as seen in Fig. 4, the second especially, in which two lateral

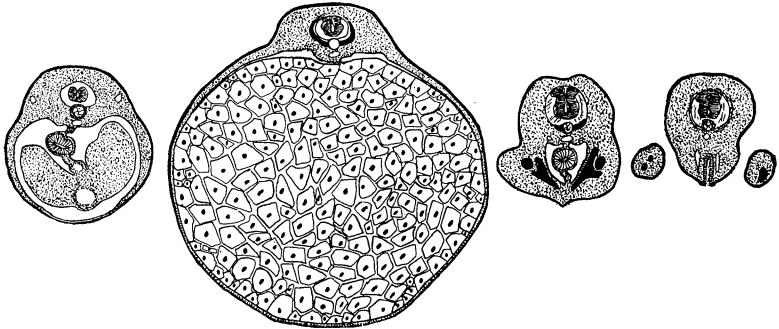


FIG. 5.—Four cross-sections from an advanced embryo of *Desmognathus fusca* [1898 material] slightly older than Fig. 4. The sections are 20 μ in thickness, and the complete series, from the tip of the nose to the end of the cloaca consists of 335 sections. The numbers affixed to the sections in the figure indicate their place in the series. $\times 15$.

cœlomic spaces may be seen dorsal to the yolk-mass, separated by a mesentery. In the first the alimentary canal (œsophagus or beginning of stomach) is suspended between dorsal and ventral mesenteries, in the latter of which lies the already well-developed liver, while in the former is seen the beginning of a pancreas. In the third section are seen the two lateral cœlomic cavities, dorsal and ventral mesenteries, the hip girdles and the heads of the femora, and in the fourth are the last (most posterior) remnants of the cœloms, the open cloaca, and the two legs, the one cut through the femur, and the other through tibia and fibula.